Effect of Peanut Plant Fungal Infection on Oviposition Preference by *Spodoptera exigua* and on Host-Searching Behavior by *Cotesia marginiventris*

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ABSTRACT In the current study, we tested the effect of peanut, *Arachis hypogaea* L. (Leguminoseae), stem infection by the white mold fungus, *Sclerotium rolfsii* Saccodes (Basidiomycetes), on the oviposition preference of beet armyworms (BAW), *Spodoptera exigua* Hübner (Lepidoptera: Noctuidae) and on the host-searching behavior by a BAW larval parasitoid *Cotesia marginiventris*. We found that, in choice tests, adult BAW oviposited more on white mold-infected plants than on healthy plants. We also found evidence that this preference is mediated by plant volatiles and other biochemical changes in plant chemistry caused by fungal infection. When plants were exposed to BAW feeding, the parasitoid *C. marginiventris* landed more frequently on infected than on healthy plants. We conducted wind tunnel choice experiments to determine whether the more frequent landing by the wasps was mediated by the volatiles emitted by healthy and white mold-infected plants in response to BAW damage. In these wind tunnel experiments, wasps were more responsive to volatiles from plants infected with the white mold compared with healthy ones, when both types of plants were exposed to damaged by BAW caterpillars. Thus, white mold-infected peanut plants were preferred by BAW for oviposition, but, when damaged by BAW larvae, infected plants were also more attractive to one of the BAW natural enemies. To our knowledge, this is the first time that the effect of pathogen-induced biochemical changes in plants on parasitoid behavior has been evaluated.

KEY WORDS *Spodoptera exigua*, tritrophic interactions, fungal infection, plant volatiles, *Cotesia marginiventris*

UNDERSTANDING SEARCHING BEHAVIOR of insect herbivores and their natural enemies is imperative for the development and deployment of sound pest management tactics. Plant-derived volatile chemicals directly affect the behavior of herbivorous and carnivorous insects. Oviposition site selection by female herbivores is mediated for the most part by chemical cues (Renwick 1989). For example, mated codling moths are attracted to apple tree branches with green fruit, and it has been demonstrated that the orientation is in response to host-emitted volatiles (Yan et al. 1999, Witzgall et al. 1999).

Herbivore-induced plant volatiles also play a major role in attracting natural enemies of the herbivorous species. For example, predatory mites, *Phytoseiulus persimilis*, have been found to be attracted to odor blends emanating from host plants damaged by their prey, *Tetranychus urticae* (Dicke and Sabelis 1988, Dicke et al. 1990). Similarly, *Spodoptera exigua* feeding on corn plants (Turlings et al. 1991a) results in volatile emissions that attract the parasitoid, *Cotesia marginiventris*, to the microhabitat of the herbivores (Turlings et al. 1991a). In fact, herbivore-induced volatile compounds released by plants have been shown to be the most important cues used by parasitoid wasps to locate their host caterpillars (Turlings et al. 1991a,b).

Volatile chemicals can also be produced by plants in response to pathogen infection. For example, infection by the fungus *Alternaria brassicae* on *Brassica rapa* seedlings induces the release of volatile compounds derived from glucosinolate degradation (Doughty et al. 1996). Also, *Phaseoulus vulgaris* releases volatile linolenic acid derivatives 15–24 h after inoculation with *Pseudomonas syringae pv. phaseolicola* (Croft et al. 1993), and *Arachis hypogaea* plants infected with the white mold fungus, *Sclerotium rolfsii*, release E-4, 8-dimethyl-1,3,7-nonatriene, methyl salicylate, and (E,E)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (Cardoza et al. 2002). Furthermore, previous pathogen infection of the plant has also been found to affect the plant-produced volatile blends it produces in response to insect damage. The volatile blend produced by white mold-infected peanut plants fed on by beet armyworm (BAW) caterpillars contained methyl salicylate and the fungus-produced 3-octanone, in ad-

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dition to those emitted by healthy plants exposed to insect feeding alone (Cardoza et al. 2002).

Many insect herbivores use plant-produced volatile compounds to locate their hosts, and their parasitoids also use plant-derived volatile chemicals to locate the herbivores. Hence, the volatiles emitted by plants in response to pathogen infection may affect oviposition site selection by herbivore females and/or the host-searching process by natural enemies,. In this study, we evaluated the effect of *S. rolfsii* infection on peanut plants on the oviposition site selection by *S. exigua* and on the landing frequency and attraction of their parasitoid *C. marginiventris* to BAW-damaged plants.

Materials and Methods

Plant and Insect Material. Georgia Green peanut seeds were provided by Drs. Tim Brenneman and Glen Raines (Coastal Plain Experiment Station, University of Georgia, Tifton, GA). Seeds were sown in pairs in 3.78-L pots (16-cm diameter) containing a 1:1 (vol: vol) mixture of commercially available filter sand and Metromix 300 (Scotts-Sierra Horticultural Company, Marysville, OH). Plants were grown in an insect-free greenhouse with natural light, under Florida summer conditions (14L:10D light cycle). The greenhouse temperature was kept between 25 and 30°C. After emergence, seedlings were thinned to one individual per pot. Each plant received 100 ml of a 3.38 g/L liquid fertilizer solution (20–20-20 [N-P-K] Peters; W. R. Grace, Fogelsville, PA) every 2 wk starting 1 wk after emergence. At the beginning of all experiments, plants were 5 wk old and had six fully developed leaves on the main stem and three fully developed leaves on each of two secondary branches.

BAW eggs and *C. marginiventris* cocoons were obtained from the rearing facilities at the United States Department of Agriculture-IBPMRL (Tifton, GA). BAW larvae were reared on a pinto-bean artificial diet following the methodology described by King and Leppla (1984). Wasps were provided with a 20% sucrose solution. All insects were kept in a biological incubator with a 14:10 (L:D) h cycle maintained at 25°C.

Fungal Culture. *S. rolfsii* (strain 80) was grown on potato dextrose agar (PDA) petri plates from original cultures provided by Dr. Tim Brenneman (Coastal Plain Experiment Station, University of Georgia). Fresh cultures were started, under sterile conditions, in our laboratory by placing sclerotia harvested from the original culture in the center of PDA media plates. Culture plates were kept in a biological incubator with a 14:10 (L:D) h cycle and maintained at 25°C and 60–70% RH° for 3 d. To inoculate the experimental plants, fungal culture plugs (5 mm diameter) were cut out of the agar plate with a number 2 cork borer.

S. rolfsii Infection on Peanuts. Peanut plants were infected with the fungus by distributing four culture plugs along the main stem. The plugs were positioned so the fungus was in direct contact with the stem. Fungal plugs were pressed against the stem so they remained in place. Each plant was then individually covered with a 3.78-L plastic storage bag (Ziploc Dow-Brands L. P., Indianapolis, IN) to provide adequate humidity and temperature conditions for fungal growth and colonization of the plant's stem. The plants were incubated for 3 d, after which time lesions of ≈1 cm long could be observed at the point of fungal contact with the stem. Control plants were similarly covered with the plastic bags, but received no fungal inoculum or agar plugs. After this incubation period, bags were removed from the plants 24 h before being used for the experiment. *S. rolfsii* is a nonsystemic pathogen (Agrios 1997), and only the stems of the plants were in contact with the fungus. Therefore, the leaves that were consumed by the caterpillars were not infected by the fungus.

BAW Oviposition on Healthy Versus Fungus-Infected Peanut. To test the free-choice oviposition preference of BAW moths, three healthy and three fungus-infected plants were placed within a 4 × 2 × 3-m (L × H × W) screen cage. Plants were distributed in two rows along the length of the cage, so there was approximately a 1-m distance in between plants. Healthy and infected plants were placed in an alternate fashion. Additionally, to account for any environmental differences within the cage, plants were moved so they were on opposite sides of the cages each day throughout the experiment. Sixteen 5- to 7-d-old adult BAW, eight females and eight males, were released in the center of the cage and were allowed access to the plants for 3 d. Insects were provided with cotton balls soaked in a 20% sucrose solution placed in the middle of the room as a source of food. At the end of the experiment, leaves from each treatment containing egg masses were removed from the plants and brought into the laboratory to determine the number of egg masses and number of individual eggs laid on plants with the two treatments. This experiment was repeated over time for a total of six replicates.

To determine whether the oviposition preference by the moths was mediated by the plants' volatile emissions, we conducted dual-choice tests in a wind tunnel. The Plexiglas tunnel used in this experiment was 2.5 × 0.6 × 0.6 m with an airflow of ≈0.2 m/s (Eller et al. 1988) and was housed in a room maintained at 28°C and ≈80% RH. Lighting was provided by four overhead incandescent lights (90 W). Healthy and fungus-infected plants were removed from the pots, and the soil around the roots was carefully removed. The roots of each plant were then wrapped with three plies of wet paper towel and placed inside a 3.78-L plastic storage bag. The entire plant was then placed in a 4-L Mason glass jar (Alltrista, Muncie, IN) fitted with a metal lid (modified as described below). Supplemental illumination for the plants was provided by a 90 W incandescent lamp from above the glass jars. The jar lids were modified by drilling two equidistantly distributed holes of ≈0.6 cm diameter. The holes were fitted with Teflon tubing so one would serve as an inlet and the other as an outlet for the air passing over the plants. The air outlet from each of the jars was connected to one of two odor sources located

at the top on the upwind end of the tunnel. Odor sources were parallel to the airflow and were 30 cm apart from one another, 8 cm from the upwind end, 13 cm from each of the walls, and ≈30 cm above the floor of the tunnel. Odors were introduced into the tunnel by a stream of humidified air passed at a rate of 500 ml/min over each plant treatment. Two healthy 1-mo-old peanut plants were placed at the upwind side of the wind tunnel and placed so that one of the plants was directly under the volatile plume coming from the treatment plant and one was directly under the volatile plume coming from the control plant. The plants inside the tunnel were healthy and similar in shape, color, and size; thus, we presume that any differences in the number of eggs laid on these plants could only be attributed to differences in the quality of the air passing over them. Eight 5- to 7-d-old adult BAW, four females and four males, were released at the downwind end of the tunnel and were allowed access to the plants for 3 d. Insects were provided with cotton balls soaked in a 20% sucrose solution placed in the center of the tunnel as a source of food. At the end of the experiment, leaves from each treatment containing egg masses were removed from the plants and brought into the laboratory to determine the number of masses laid on plants with the two treatments. In our previous experiment, the number of individual eggs was correlated with the number of egg masses (Y.J.C., data not shown); thus, the number of individual eggs was not determined in this and the following experiment. This experiment was repeated over time, using different sets of insects and plants, for a total of five replicates.

Finally, to determine whether moth oviposition preference was mediated by surface and/or internal changes in the plants, we conducted dual-choice oviposition experiments. In these experiments, two plants, one healthy and one fungus infected, were placed side by side within $46 \times 46 \times 46$-cm Plexiglas cages. The cages were big enough to snugly accommodate the two plants, and the plants were placed so that their canopies overlapped each other. Six 5- to 7-d-old adult BAW, three females and three males, were released inside the cage and were allowed access to the plants for 3 d. Insects were provided with cotton balls soaked in a 20% sucrose solution placed in the center of the cage as a source of food. At the end of the experiment, the number of egg masses on leaves from plants under each of the treatments was counted and recorded. This experiment was repeated over time, using different sets of insects and plants, for a total of six replicates.

Response of *C. marginiventris* to Healthy and *S. rolfsii*-Infected Peanuts Damaged by BAW. To test the effect of white mold infection on peanut attraction to BAW larval parasitoids, infected and healthy peanut plants were exposed to feeding by 10 third instar BAW larvae for 24 h. After this feeding exposure, insects were removed from the plants, and one healthy and one white mold-infected plant were placed 1 m apart in a $2.5 \times 0.6 \times 0.6$-m (L $\times$ H $\times$ W) Plexiglas cage. Ten 3- to 5-d-old mated female parasitoids were released in the middle of the cage. Parasitoids needed ≈20–30 min to adjust to the new environment before responding to the plants. During this time, insects were observed exiting the container in which they were introduced and interacting with each other while hanging from the top of the cage. After the adjustment period, insects were watched for an additional 15 min, during which the number landing on each of the plants was recorded. At the end of the observation period, insects were removed from the cage, the position of the plants was switched, and a new set of insects was introduced, allowed to settle for ≈30 min, and watched for another 15 min. This procedure was repeated twice more during the same day, with the same set of plants and with a total of four wasp sets. This experiment was repeated three more times at different times with different sets of plants and insects. All experiments were conducted in the period between 9:00 a.m. and 4:00 p.m.

To determine whether the landing preference by the parasitoids was mediated by the plants' volatile emissions, we conducted dual-choice tests in the wind tunnel described above. The odor source used consisted of healthy or fungus-infected peanut plants exposed to feeding by 15 third instar BAW 12 h before the beginning of the experiment. Wasps used for this experiment were 3- to 5-d-old mated females. To ensure the insects' response to peanut plant odors, wasps were provided a stinging experience on second and third instar BAW feeding on healthy peanut leaves 12 h before being used in the bioassay. Insects responding to each of the odor sources were trapped on 10-cm-diameter circles made out of light green adhesive paper (Atlantic Paste and Glue, Brooklyn, NY). A hole was cut in the center of the circle so it could be fitted around the odor source tubing. Sets of 10 wasps were introduced ≈1.5 m downwind and centered so that insects would come in contact with plumes from both odor sources. Insects were released 12:00–2:00 p.m. and were allowed to remain in the tunnel for 18–20 h, at which time the number of insects caught on each of the sources was counted and recorded. Insects within the tunnel were provided with a cotton ball soaked in a 20% sucrose solution placed at the site of release as a source of food. The odor sources were switched before each bioassay to account for any variation in environmental conditions within the tunnel. This experiment was repeated over time, using different sets of plants and insects, to obtain a total of eight replicates.

In preliminary tests, parasitoid wasps did not land on, nor respond to volatiles from healthy or fungus-infected peanut plants that were not exposed to BAW damage; therefore, these data could not be included as part of the current study.

Statistical Analyses. Data for BAW oviposition preference were analyzed by paired *t*-test (Proc MEANS, SAS Institute 1996). Paired *t*-test (Proc MEANS, SAS Institute 1996) was also used to analyze data on parasitoid wind tunnel responses. Data on parasitoid landing were analyzed using a likelihood of χ^2 test (*G*-test, Proc FREQ, SAS Institute 1996).
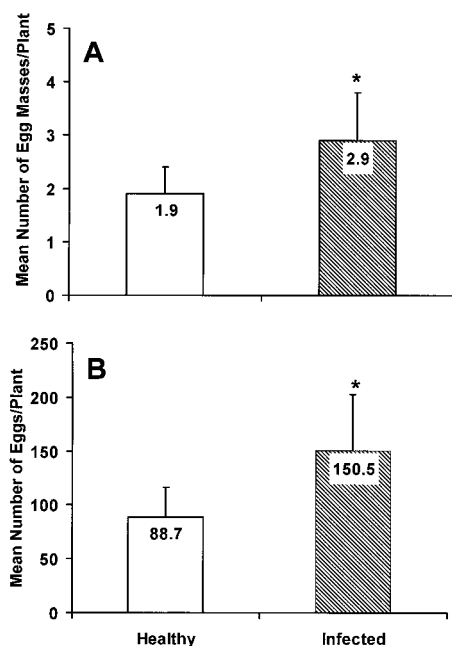
Fig. 1. Oviposition preference by *S. exigua* in choice tests in a screen cage with three healthy (open bars) and three white mold-infected (filled bars) peanut plants. (A) Mean number of egg masses per plant, and (B) mean number of eggs per plant. Error bars denote 1 SE ($n = 6$), and * denotes significant differences based on paired *t*-test analysis, $P \leq 0.05$.

Fig. 2. Oviposition preference by *S. exigua* in choice tests with healthy (open bars) and white mold-infected (filled bars) peanut plants. (A) Mean number of egg masses per plant in the Plexiglas cage dual-choice experiment, and (B) mean number of egg masses per plant in dual-choice wind tunnel experiments. Error bars denote 1 SE ($n = 6$ and 5 for A and B, respectively), and * denotes significant differences based on paired *t*-test analyses, $P \leq 0.05$.

Results

In the screen room free-choice experiment, adult BAW laid significantly more eggs on peanut plants that were infected by the white mold compared with healthy ones ($t = 8.01$, df = 5, $P = 0.034$) (Fig. 1, A and B). On average, BAW laid ≈1.7 egg masses and 60 eggs more on peanut plants infected with the white mold fungus than they did on healthy plants. The oviposition preference for fungus-infected peanut plants was also prevalent in both the Plexiglas cage ($t = 10.01$, df = 5, $P = 0.014$) and wind tunnel dual-choice ($t = 3.45$, df = 4, $P = 0.0038$) experiments. In the Plexiglas cage experiments, BAW laid ≈175% more egg masses on infected compared with healthy plants (Fig. 2A). Similarly, in the wind tunnel experiments, BAW laid ≈150% more masses on healthy peanut plants under the volatile plume from fungus-infected peanut compared with healthy plants under the volatile plume from uninfected peanut (Fig. 2B).

In Plexiglas cages, with one white mold-infected and one healthy plant, the BAW larval parasitoid *C. marginiventris* landed significantly more on infected BAW-damaged plants that were damaged by BAW larvae when plants were also white mold infected than on plants when they were healthy and BAW damaged ($G = 826.61$, df = 5, $P = 0.0001$) (Fig. 3A). On average, three more landings were observed on plants infected with the fungus compared with healthy ones. Similarly, in the wind tunnel ex-
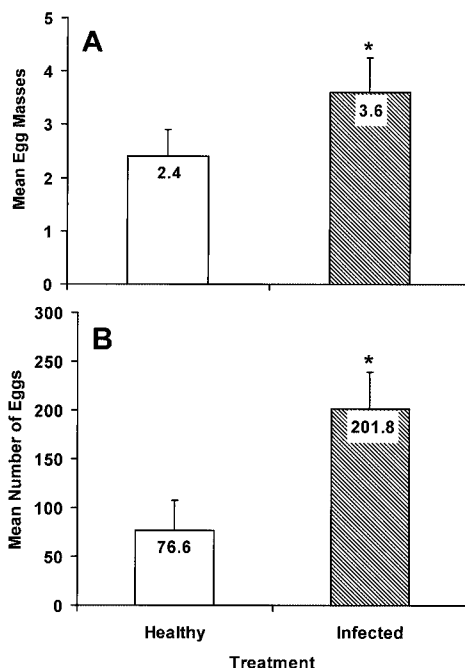
periment, over 300% more wasps responded to infected, BAW-damaged plant odors compared with odors originating from healthy, BAW-damaged plants ($t = 10.17$, df = 7, $P < 0.0001$) (Fig. 3B).

Discussion

Attraction of phytophagous insects and their natural enemies to their respective hosts involves both olfactory and visual cues. Attraction from long distances or during the scotophase, when visual cues are not available or easily perceived, may rely heavily on smell. Thus, olfactory cues are powerful and may be the most important stimuli during this phase of host searching (Huang and Renwick 1993, Renwick and Chew 1994, Turlings et al. 1990, Röse et al. 1996, Dicke and van Loon 2000). After the insect has landed on the plant, the evaluation of physical and chemical characteristics of the plant tissue will help in the final decision making by the phytophagous insects before either feeding or oviposition takes place. Plant cells contain large numbers of different chemicals, and some may stimulate while others may deter insects from feeding or ovipositing on a given plant.

Peanut plants infected with the white mold fungus, *S. rolfsii*, have higher levels of soluble sugars and lower levels of soluble phenolics, which may result in increased feeding preference and performance by BAW
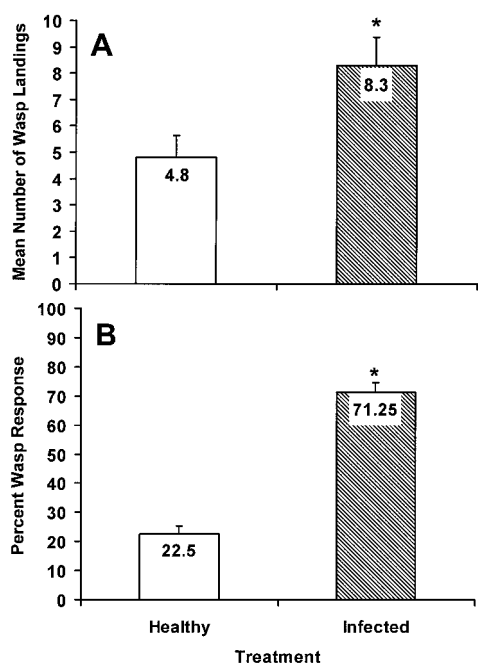
Fig. 3. Response of the BAW parasitoid *C. marginiventris* in choice tests with healthy, BAW-damaged (open bars), and white mold-infected (filled bars) BAW-damaged plants fed on by BAW. (A) Landing preference on plantsin Plexiglas cages with one healthy and one infected plant, and (B) wind tunnel response to odors of healthy, BAW-damaged and infected, BAW-damaged plant odors. Error bars denote one SE ($n = 6$ and 8 for A and B, respectively), and * denotes significant differences based on *G*-test for A and paired *t*-test for B, $P \leq 0.05$.

larvae (Cardoza et al. 2002, 2003, Cardoza 2002). These internal biochemical changes may also explain the increased BAW oviposition on fungus-infected peanut observed in the current study. In addition to changes in internal physiology caused by pathogen attack, plants may also release volatile substances. For example, peanut plants infected with the white mold fungus release a set of compounds that differs significantly from that of healthy plants and plants that are damaged by BAW (Cardoza et al. 2002, Cardoza 2002). Thus, the internal and external expressions of biochemical changes induced in plants by pathogen infection may play a role in oviposition site selection by herbivore females. In the current study, we found that *S. exigua* laid more eggs on white mold-infected peanut plants than healthy ones. In this experiment, however, olfactory, visual, and tactile cues could all have contributed to the insect's final selection. Therefore, additional experiments were performed to determine whether oviposition site selection by these insects was caused by the difference in volatile emissions between healthy and white mold-infected peanut plants. Our Plexiglas cage results show clearly that BAW prefer to oviposit on fungus-infected plants even if their use of volatile plumes for orientation and identification of host plants is significantly restricted. This indicates

that internal and/or surface changes induced in the plants by fungal infection are responsible for the preference observed in our free-choice experiments. Furthermore, the volatiles emitted by fungus-infected plants are also important for host finding and oviposition host selection by BAW, as shown in our wind tunnel choice experiments.

Plant volatile compounds play a major role in guiding the host-searching behavior by natural enemies (Turlings et al. 1991a,b, Tumlinson et al. 1993, Röse et al. 1998, Kessler and Baldwin 2001). These chemical signals may derive from the herbivore host (Vinson 1976, Van Alphen and Vet 1986), from the intact plants (Vinson 1976), or from the herbivore-damaged plant. Herbivores have evolved ways to evade their natural enemies; thus, they emit very few volatile cues that parasitoids can use to locate them. Therefore, long distance location of prey by parasitoids seems to be dependent upon information provided by other sources, such as the host plants the herbivores are feeding upon. Female herbivores select oviposition sites that not only provide the best suitable food for their brood, but also minimize exposure to natural enemies (Faeth 1986, Godfray 1994). Adult BAW oviposited more, and their larvae fed more and performed better on fungus-infected peanuts (Cardoza et al. 2002). Then, could it also follow that feeding on infected plants helps BAW avoid natural enemies? To test this hypothesis, we conducted dual-choice experiments to determine whether peanut plant infection by *S. rolfsii* had any negative effect on the parasitoid's ability to find diseased plants fed on by BAW. In a dual-choice situation, *C. marginivetris* were observed landing with significantly higher frequency on peanut plants that were infected by the fungus and then exposed to BAW larval feeding. In a previous study, we reported that BAW preferred and consumed larger amounts of leaves from white mold-infected peanut plants (Cardoza et al. 2002). Also, white mold-infected plants release greater amounts of some volatile compounds compared with healthy ones (Cardoza et al. 2002, Cardoza 2002). We believe that the greater release of volatile compounds associated with BAW leaf consumption may be responsible for the preferential landing on, and greater response to peanut-infected plants by *C. marginiventris.*

Manipulation of insect herbivores and their natural enemies has potential applications for the control of agricultural pests in today's agriculture. To exploit this potential in an economical and practical manner, we must first understand the biology and behavior of the insects and their interactions with their respective hosts. Several studies have evaluated the effect of plant pathogen infection on feeding and performance of insect herbivores (Kluth et al. 2001, Hatcher et al. 1994, Kruess 2002, Moran 1998). However, the nature of plant-pathogen-insect interactions is highly variable, and the outcome may be beneficial or detrimental depending on the species involved (Hatcher 1995, Kluth et al. 2001). Apart from the results presented in this work, Friedli and Bacher (2001) is the only study we are aware of in which the effect of plant disease on

oviposition preference by the herbivore has been tested. The latter study also reported a positive correlation between rust infection of creeping thistle, *Circium arvense*, and oviposition by female weevils, *Apion onopordi*. To our knowledge, ours is the first study to evaluate the effect of pathogen-induced biochemical changes in plants on parasitoid behavior. Results from our studies show clearly that, while infected plants are favored by BAW for oviposition, and even though BAW larval development has been previously shown to be enhanced on such plants (Cardoza et al. 2003), white mold-infected plants do not provide protection against one of the BAW natural enemies. To the contrary, infected peanuts exposed to BAW damage were significantly more attractive to *C. marginiventris* than healthy plants. These are all ecologically significant findings demonstrating that phytopathogen-induced changes in plant chemistry modulate plant-insect interactions, not only at the second, but also at the third trophic level.

Acknowledgments

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